Habitat Segregation of *Banksia* Shrubs at Gibraltar Range National Park

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Events during seedling recruitment affect species' distributions, causing habitat segregation of congeneric species within the same area. We documented the segregation of *Banksia marginata* and *B. spinulosa* var. *neoanglica* in adjacent swamp and woodland habitats at two sites by surveying adult and seedling distributions. We also examined seed banks and seed characters as factors contributing to segregation. Habitat segregation was pronounced, with 92% of *B. marginata* adults located in swamps and 98% of *B. spinulosa* adults located in woodlands. After fire, 84% of *B. marginata* seedlings were in swamps, but 10 months later this increased to 93%, indicating that although seeds dispersed to and germinated in adjacent woodlands, most seedlings failed to establish. Seedlings of *B. spinulosa* were confined to woodlands, indicating that seeds did not disperse into swamps or that, if they did, seeds failed to germinate or seedlings suffered early mortality. Canopy seed banks of both species were large (> 280 seeds/plant) and seeds of both species possess membranous wings, allowing dispersal between habitats. Overall, neither limited numbers of seeds nor limited seed dispersal are likely to cause habitat segregation. Instead, processes occurring during early seedling growth are probably more influential.

INTRODUCTION

Seedling recruitment is a critical stage in the demography of plant populations. Seeds and seedlings typically experience high mortality rates, and events during recruitment potentially affect the distribution of species in the landscape (Harper 1977; Grime 1979; Silvertown and Charlesworth 2001). When seeds are dispersed, they encounter a variety of abiotic and biotic conditions that affect the seed germination, seedling emergence, survival or growth stages of the life cycle. Interactions between these factors exert powerful effects on the spatial patterns of recruitment, allowing regeneration to occur in some microhabitats but not others (Lamont et al. 1989; Mustart and Cowling 1993; Schütz et al. 2002; Castro et al. 2004). Grubb (1977) coined the term "regeneration niche" to distinguish between the habitat conditions required for seedling recruitment as opposed to adult survival and reproduction. The regeneration niche is generally considered to be more complex than the niche experienced by adult plants, providing substantial opportunities to explain the distribution patterns of different species (Grubb 1977).

Habitat segregation of congeneric species in distinct habitats within the same general geographic area is a common feature of coastal plains and tableland areas of southern Australia (Siddiqi et al. 1972; Bowman et al. 1986; Keith and Myerscough 1993; Myerscough et al. 1995; Clarke 2002), and has been well documented in *Banksia*. On the Swan coastal sand plain near Perth, *Banksia littoralis* is restricted to swamp margins, whereas *B. menziesii* and *B. attenuata* occur more widely in drier woodland areas (Groom et al. 2001). Further north of Perth on the Eneabba sandplain, *B. hookeriana*, *B. prionotes* and *B. attenuata* are segregated along topographic gradients in the dune-swale system (Lamont et al. 1989; Groeneveld et al. 2002). In NSW, on the coastal sand plains in the Myall Lakes area, *B. oblongifolia* and *B. aemula* are segregated into either wet heath or dry heath occurring on the slopes and ridges, respectively (Myerscough et al. 1996). Finally, on the north coast of NSW, *B. ericifolia* is most common

in wet heath, while its congener *B. aemula* occurs in headland heath, dry heath and moist heath (Benwell 1998). Although such patterns have been attributed to physiological intolerance and competition at later life-cycle stages, increasing evidence points to the importance of processes occurring during recruitment in mediating segregation (Myerscough et al. 1996; Clarke et al. 1996; Williams and Clarke 1997). Using field experiments Myerscough et al. (1996) and Clarke et al. (1996) demonstrated that segregation of *B. aemula* and *B. oblongifolia* at Myall Lakes was related to processes operating during seed dispersal when safe sites for seeds are required, and during establishment when resources are critical for early seedling growth.

At Gibraltar Range National Park (GRNP), sedge-heath communities occur in areas of impeded drainage on hillsides and on flats that are surrounded by a matrix of sclerophyll woodland. Segregation of congeneric species into either sedge-heath or woodland habitats is common (Sheringham and Hunter 2002). Here we quantified the distribution of both adult and seedling populations of *Banksia marginata* and *B. spinulosa* var. *neoanglica* to determine whether the two species are segregated and whether processes operating during recruitment mediate this pattern. We found pronounced segregation that is established during recruitment, and to explain the observed distribution pattern we examined the seed production and seed dispersal stages of the life cycle. Specifically, we examined seed bank size and seed attributes to determine whether both species produce viable seeds and whether seeds have the potential to disperse between habitats.

MATERIALS AND METHODS

Study species

Banksia marginata Cav. is widely distributed along the coast and ranges of south-eastern Australia. At GRNP, the species is at the northern limit of its range (Harden 2002). In this area, plants are killed by fire and populations rely solely on seeds for recovery (i.e. are obligate seeders, Vaughton and Ramsey 1998; Benson and McDougall 2000). Adult plants are single-stemmed and grow to 2 m in height. The inflorescences are 5-10 cm long and bear straight styles. Flowers are self-compatible and two seeds are usually formed per follicle (Vaughton and Ramsey 1998, 2006). At this site follicles are strongly serotinous and open only after exposure to high temperatures during fires. Seeds have a membranous wing, allowing wind

dispersal. Most seedling recruitment occurs in the first 12 months after fire.

Banksia spinulosa Sm. var. *neoanglica* A.S. George (*B. cunninghamii* Sieber ex Rchb. subsp. A; Harden 2002; hereafter *B. spinulosa*) is found in northern NSW and southern Queensland. Plants have an underground lignotuber and are able to resprout after fire (i.e. are resprouting). Adult plants are multistemmed and grow to 2 m in height. The inflorescences are 6-15 cm long and bear hooked styles. Flowers are self-compatible, but most seeds are outcrossed (Vaughton and Carthew 1993). The follicles are strongly serotinous and have a single winged seed (Vaughton and Ramsey 2001). Seedling recruitment occurs after fire.

Study sites

Two sites were chosen at GRNP that were burned by bushfires during November 2002: Waratah Trig (WT: 29o29' S, 152o19' E, 1050 m a.s.l.) and Surveyors Creek (SC: 29o32' S, 152o18' E, 1044 m a.s.l.). These sites occur on separate drainage channels and are approximately 5 km apart. Both sites are floristically and structurally similar, comprising two associated vegetation types, sclerophyll woodland and sedge-heath. The woodlands are dominated by *Eucalyptus olida* with a diverse shrub understorey. The sedge heaths are dominated by *Lepidosperma limicola* with emergent shrub species occurring along the swamp margins (Sheringham and Hunter 2002).

Distribution of adults and seedlings

For both species, the distributions of adult plants were surveyed 3 months after the fire. Burnt adults retained their cones, and were readily identified. Seedling distributions were surveyed twice, at 18 and 28 months after the fire. Seedlings of the two species were identified by differences in cotyledon and leaf traits.

We used stratified belt-transects for the adult and seedling surveys. Different transects were used for each survey, ensuring samples were independent of each other. Transects spanned 40 m of the swamp habitat and 60 m of the woodland habitat, and were haphazardly placed. This stratification ensured that we surveyed the distributions of both *B. marginata* and *B. spinulosa*. Transects excluded the wetter regions of the swamp where banksias rarely occur (Sheringham and Hunter 2002). For adult and seedling surveys at each site, four, 5 m wide transects and six, 1 m wide transects were used, respectively. Within transects, all banksias were counted and recorded as being in either
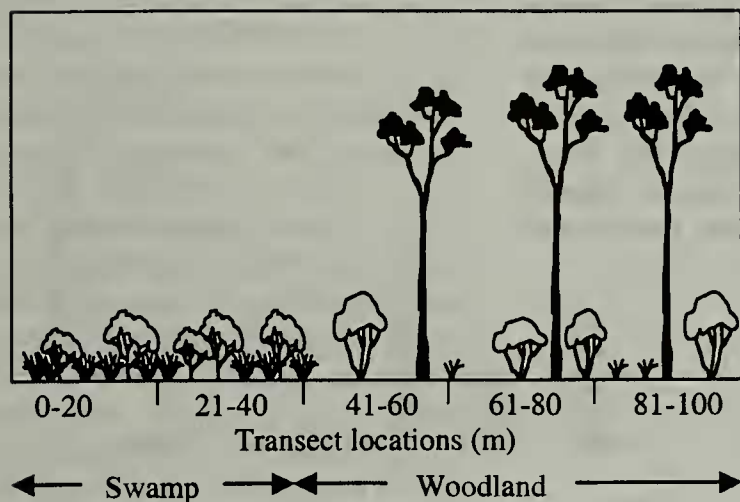
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Figure 1. Vegetation profile of the swamp and woodland association and the placement of stratified belt-transects used to examine the distribution of _B. marginata_ and _B. spinulosa_ at the SC and WT sites. The illustration is representative of the vegetation and is not drawn to scale.

the swamp or woodland habitat (Fig. 1).

To assess habitat segregation of _B. marginata_ and _B. spinulosa_, we calculated an analysis of deviance using a logit model with a binomial error term and a logit link function. The three explanatory variables were site (SC, WT), plant age (adults, seedlings at 18 and 24 months after the fire) and habitat (swamp, woodland). The response variable was the number of plants of one species expressed as a proportion of the sum of the number of plants of both _Banksia_ species. With this approach, the explanatory variables and their interactions are interpreted as their effect on the response variable in a similar fashion to ANOVA. In preliminary analyses, the three-way interaction (site x habitat x age) and the site x age interaction were not significant and were omitted from the final model ($P > 0.50$). We also calculated the percentage of the total deviance explained by each term. Because the age x habitat interaction was significant in the final model, we also examined how the distributions of adults and seedlings differed with respect to habitat for each species at each site using 3 x 2 contingency tables (G-tests). A significant G-test indicates that the distribution of plants of the different ages depends on habitat. We used a sequential Bonferroni correction to account for multiple tests.

Seed bank

We estimated the seed bank (seeds/m^2) of each species as: (plants/m^2) x (mean number of cones/plant) x (mean number of viable seeds/cone).

Similarly, the number of seeds per plant was estimated as the product of cones per plant and seeds per cone. Plant density was assessed using five haphazardly placed quadrats in each habitat at each site. In swamp and woodland habitats, 5 m x 5 m and 10 m x 10 m quadrats were used, respectively, to ensure both species were adequately represented. To assess the number of cones per plant, we counted cones with follicles on 50 plants of each species per site. For the number of viable seeds, we collected five cones from each of 20 plants of each species per site prior to the fire in August 2002. Seeds were extracted in April 2003 by heating cones for 30 min in an oven set at 110 °C. Seeds were deemed viable if they were intact and plump.

Seed dispersal

To assess the dispersal potential of seeds, seed mass:seed area ratios (i.e. wing loading) were calculated; larger wing loadings imply shorter potential dispersal distances. Seeds were weighed and measured with the seed and wing intact, using three seeds from each of 10 plants per species from each site. Seeds were weighed to the nearest 0.1 mg, and seed area was determined using a leaf area meter (Δ T Area Meter, Delta – T Devices).

Seed bank and dispersal analyses

Data were analysed with two-way ANOVAs, with species as a fixed factor and site as a random factor. When the site x species interaction was not significant ($P > 0.2$), it was pooled with the error term, resulting in a more powerful test of the differences between species (Quinn and Keough 2002). When the site x species interaction was significant, we calculated tests of simple main effects comparing the species at each site. To meet assumptions of ANOVA, plant density, the numbers of cones, seed mass and wing loadings were log$_{10}$ transformed. Other variables did not require transformation.

RESULTS

Distribution of adults and seedlings

Of the 3610 plants found on transects, 15.5% and 61.7% were _B. marginata_ adults and seedlings, respectively, and 3.2% and 19.6% were _B. spinulosa_ adults and seedlings, respectively. The final logit model included the three main effects, and the age x habitat and the site x habitat interactions (Table 1). The significant age x habitat interaction indicates

Table 1. Analysis of deviance (logit model) examining the distribution of *Banksia marginata* and *B. spinulosa* adults and seedlings (18 and 28 months after the fire) in swamp and woodland habitats at the SC and WT sites (n = 3610 plants). Habitat explained 97.7% of the total deviance. The site x habitat x age and the site x age interactions were not significant (P > 0.50), and they were omitted from the final model.

Source	df	Δ Deviance	P
Site	1	32.71	< 0.0001
Habitat	1	2505	< 0.0001
Age	2	11.33	0.003
Age x habitat	2	12.34	0.002
Site x habitat	1	2.97	0.085

that the relative frequencies of adults and seedlings varied between the two habitats (Table 1, Fig. 2). Although the main effects of site, age and habitat were significant, habitat singularly explained 97.7% of the deviance in the model (Table 1), indicating that the two species exhibited pronounced habitat segregation. Overall, most *B. marginata* plants of all ages were found in the swamps (≥ 84%) and most *B. spinulosa* plants were found in the woodland (≥ 95%).

For *B. marginata*, adult and seedling distributions differed significantly at both sites (Table 2, Fig. 2). Seedlings were distributed more widely than adults 18 months after the fire, but by 28 months, the distributions were similar. At 18 months, about 84% and 16% of seedlings were found in the swamps and woodlands, respectively, but 10 months later, about 93% and 7% of seedlings were in the two habitats, respectively. For *B. spinulosa*, adult and seedling distributions at WT did not differ significantly (Table 2, Fig. 2). At SC, however, adults were distributed more widely than seedlings (Table 2, Fig. 2). About 5% of adults were located in the swamp, whereas > 99% seedlings were confined to the woodland.

Seed bank

For plant density (plants/m^2), the site x species interaction was not significant ($F_{1,16}$ = 0.48, P > 0.450), and it was pooled with the error term for the final analysis. Sites did not differ ($F_{1,17}$ = 0.07, P > 0.750), but *B. marginata* plants were about 10-fold more

numerous than *B. spinulosa* plants ($F_{1,17}$ = 173.67, P < 0.001; Table 3). For the number of cones per plant and viable seeds per cone, the site x species interaction was significant (cones: $F_{1,196}$ = 16.85, P < 0.001; seeds: $F_{1,196}$ = 21.15, P < 0.001), and we examined the simple main effects of species at each site. The number of cones produced by *B. marginata* was significantly greater than *B. spinulosa* at both sites (WT: $F_{1,196}$ = 103.49, P < 0.001; SC: $F_{1,196}$ = 19.08, P < 0.001; Table 3). For the number of seeds per cone, *B. marginata* produced more seeds than *B. spinulosa* at WT ($F_{1,76}$ = 24.25, P < 0.001), but at SC seed production of both species was similar ($F_{1,76}$ = 2.49, P = 0.109; Table 3). Overall, *B. marginata* plants produced about 9-fold and 1.4-fold more seeds than did *B. spinulosa* plants at WT and SC, respectively. Similarly, the seed bank (seeds/m^2) of *B. marginata* was 182-fold and 18-fold greater than that of *B. spinulosa* at WT and SC, respectively, the large differences resulting from differences in plant density.

Seed dispersal

For seed mass and seed area, the site x species interactions were significant (seed mass: $F_{1,116}$ = 11.13, P < 0.001; seed area: $F_{1,116}$ = 15.06, P < 0.001), and we examined simple main effects of species at each site. Seeds of *B. spinulosa* weighed at least 22% more than *B. marginata* seeds at both sites (WT: $F_{1,116}$ =

Table 2. Results of 3 x 2 contingency analyses examining the effects of habitat on the distribution of plants of different ages. We compared the distributions of adults (A) versus seedlings surveyed 18 and 28 months after the fire (S1 and S2, respectively) between swamps and woodlands for *Banksia marginata* and *B. spinulosa* at the SC and WT sites. G- and P-values are presented. G-values are significant following Bonferroni correction at P = 0.0125. All df = 2.

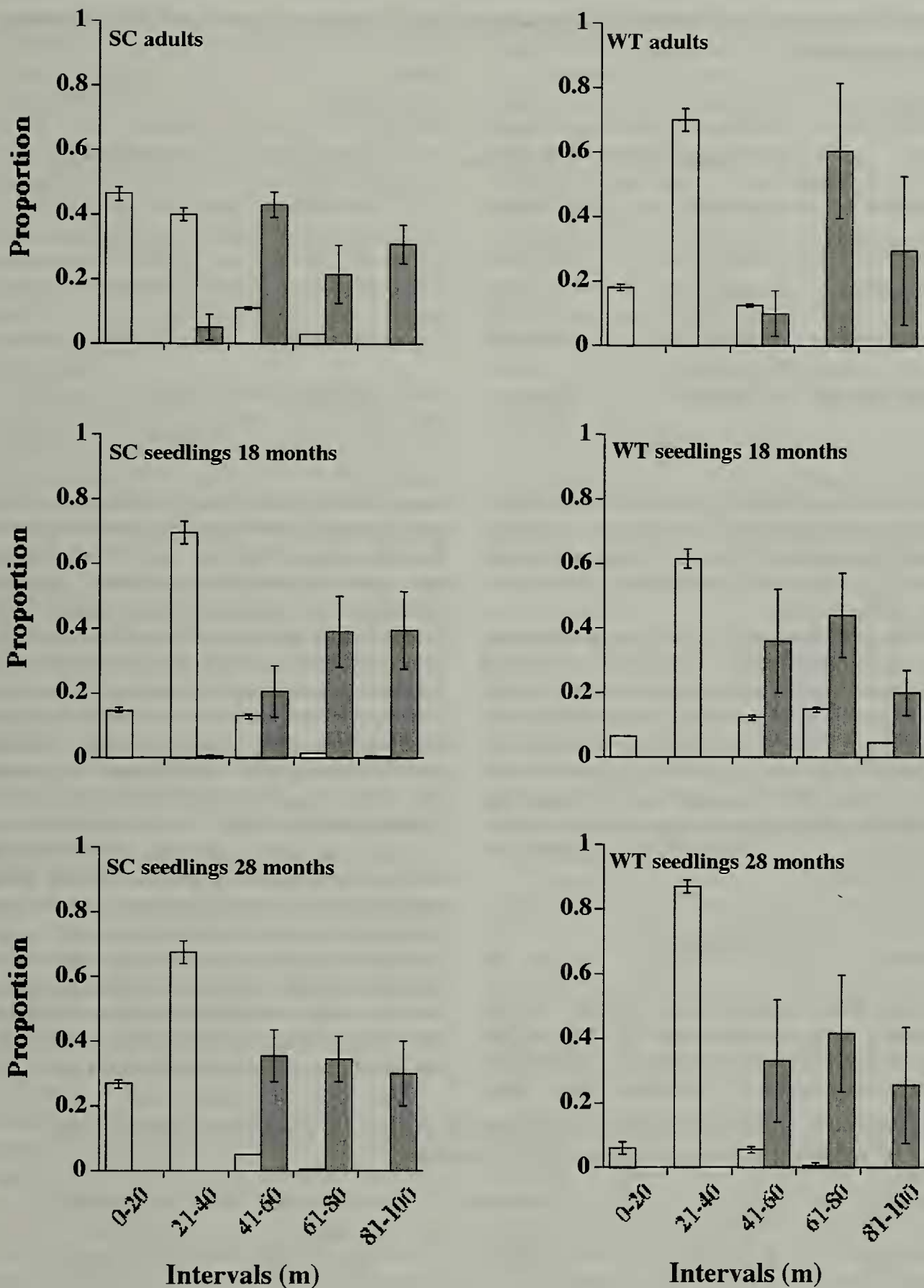| Population		*B. marginata*	*B. spinulosa*
		A vs S$_1$ vs S$_2$	A vs S$_1$ vs S$_2$
SC	G	17.54	10.07
	P	0.0002	0.0065
WT	G	23.27	0.15
	P	< 0.0001	0.926

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Figure 2. Distribution of *Banksia marginata* (open) and *B. spinulosa* (shaded) adults and seedlings at the SC and WT sites. Adults were surveyed 3 months after the fire, and seedlings were surveyed 18 and 28 months after the fire. Data are mean proportions of plants (± SE) at 20 m intervals based on four transects for adults and six transects for seedlings. The 0-20 m and 21-40 m intervals were in swamp habitats and the other three intervals were in woodland habitats.

Table 3. Seed bank characters for *Banksia marginata* and *B. spinulosa* at the SC and WT sites. Data are means ± SE.

Characters	SC		WT	
	B. marginata	*B. spinulosa*	*B. marginata*	*B. spinulosa*
Plants/m^2	0.9 ± 0.2	0.1 ± 0.1	1.0 ± 0.3	0.1 ± 0.1
Cones/plant	17.2 ± 1.8	9.2 ± 1.2	45.8 ± 4.5	9.4 ± 0.9
Seeds/cone	24.4 ± 3.8	33.3 ± 3.8	57.7 ± 3.5	30.0 ± 4.7
Seeds/plant	420 ± 72	306 ± 45	2642 ± 220	282 ± 47
Total seeds/m^2	386 ± 53	21 ± 2	2736 ± 271	15 ± 2

15.74, $P < 0.001$; SC: $F_{1,116} = 75.42$, $P < 0.001$; Table 4). By contrast, *B. marginata* seeds were at least 11% greater in area than *B. spinulosa* seeds at both sites (WT: $F_{1,116} = 51.47$, $P < 0.001$; SC: $F_{1,116} = 2.84$, $P < 0.01$; Table 4).

For wing loading, the site x species interaction was not significant ($F_{1,116} = 1.51$, $P > 0.20$), and it was pooled with the error term for the final analyses. No differences in wing loadings were found between sites ($F_{1,117} = 2.04$, $P = 0.156$). Wing loadings of *B. spinulosa* seeds were significantly greater than the wing loadings of *B. marginata* seeds, indicating that *B. spinulosa* should disperse shorter distances than *B. marginata* ($F_{1,117} = 201.06$, $P < 0.001$; Table 4).

DISCUSSION

Our results showed that *B. marginata* and *B. spinulosa* were segregated into different habitats, and that this pattern was established during seedling recruitment. Adult *B. marginata* plants were concentrated in the swamp margins, whereas *B. spinulosa* plants were located in the woodland. In *B. marginata*, seedlings were more widely dispersed than adults 18 months after fire, but by 28 months the distribution of seedlings had contracted so that it did not differ from that of adults. In *B. spinulosa*, virtually all seedlings were confined to the woodland habitats. Our results are consistent with other studies showing the importance of the regeneration niche in determining patterns of segregation of congeneric species (Lamont et al. 1989; Mustart and Cowling 1993; Myerscough et al. 1996; Clarke et al. 1996; Williams and Clarke 1997; Schütz et al. 2002).

In *B. marginata*, processes operating during seedling establishment appear to mediate habitat segregation. The wider distribution of *B. marginata* seedlings than adults 18 months but not 28 months after fire, indicates that seeds dispersed into the woodland and germinated, but seedlings failed to establish. Other studies have shown that recruitment of *Banksia* seedlings is strongly influenced by abiotic conditions, especially drought (Lamont et al. 1989;

Table 4. Seed characters relevant to dispersal for *Banksia marginata* and *B. spinulosa* at the SC and WT sites. Data are means ± SE (n = 30 seeds).

Site	Species	Seed mass (mg)	Seed area (cm^2)	Wing loading (mg/cm^2)
SC	*B. marginata*	8.44 ± 0.31	0.72 ± 0.04	11.95 ± 0.49
	B. spinulosa	12.85 ± 0.44	0.65 ± 0.07	19.56 ± 1.04
WT	*B. marginata*	8.85 ± 0.22	0.85 ± 0.03	10.64 ± 0.33
	B. spinulosa	10.81 ± 0.32	0.57 ± 0.04	18.51 ± 1.07

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Myerscough et al. 1996; Lamont and Groom 1998). At GRNP, soils in both the swamp and woodland habitats are of granitic origin. However, the swamp soils are fine textured and poorly drained compared with the more well-drained soils of the woodland (Virgona 2004). Segregation therefore may be driven by adaptation to the particular abiotic conditions in the swamp and intolerance to conditions in the woodland. Specifically, compared with *B. spinulosa*, *B. marginata* seedlings may be less tolerant of fluctuating levels of soil moisture and thus the overall drier soils in the woodland. Manipulative field and glasshouse experiments are now needed to investigate this possibility.

As expected of an obligate seeder that relies solely on seeds for recruitment (Lamont and Groom 1998; Lamont and Wiens 2003), *B. marginata* maintained a large canopy seed bank. Compared with *B. spinulosa*, adult *B. marginata* plants had 2-4 times more cones per plant, and at WT, more viable seeds per cone. *Banksia marginata* adults also occurred at higher densities than did *B. spinulosa*, resulting in seed densities that were 18-182 times greater in their preferred habitat. High seed densities provide maximum opportunities for seedling recruitment and also allow colonisation of new sites, as evidenced by the occurrence of *B. marginata* seedlings in woodland habitat 18 months after fire. Populations of obligate seeding plants, however, are susceptible to either short or very long fire intervals that can decrease the amount of stored seeds for recruitment and hence threaten population persistence (Morrison et al. 1995; Enright et al. 1996). The effect of fire on demographic processes may therefore interact with other abiotic and biotic factors influencing segregation in fire-prone heaths and woodlands such as those occurring at GRNP.

In *B. spinulosa*, > 99% of seedlings were located in the woodland 18 months after the fire. The lack of recruitment into swamps indicates that either seed availability was limited, seeds did not disperse into the swamps or seeds dispersed, but seedlings failed to establish. Although at present we are unable to distinguish between these possibilities, we suspect the latter. First, recruitment by *B. spinulosa* in swamps was unlikely to be limited by seed availability. Compared with other resprouting *Banksia* species, adult *B. spinulosa* plants maintained a large store of seeds in their canopy prior to the fire (~ 300 seeds for *B. spinulosa* vs ≤ 16 seeds, n = 7 species, Lamont and Groom 1998). Further, seedling recruitment occurred in woodland but not adjacent to swamp habitats, indicating that seed availability was adequate. Second, the inability of seeds to disperse from the woodland is unlikely to account for the absence of seedlings in

the swamps. Although *B. spinulosa* seeds had larger wing loadings (greater mass but smaller area) than *B. marginata* seeds, this may not overly affect their dispersal potential. Using wind-tunnel and seed-release experiments, Hammill et al. (1998) reported that *Banksia* seeds weighing between 9 mg and 70 mg dispersed similar distances. They found that seeds of *Banksia* species with similar characteristics to those of *B. spinulosa* and *B. marginata* were most abundant within 2-3 m of parent plants, but were readily dispersed 9-12 m and occasionally up to 40 m from parents. Assuming that *B. spinulosa* seeds behave as in Hammill's study, the absence of seedlings in the swamps is unlikely to be due to the inability of seeds to disperse the short distance from the woodland to the swamp margins.

At SC, about 5% of *B. spinulosa* adults were located in the swamp, but no seedlings were found in this habitat. These adult plants had canopy seed banks and would have released their seeds directly into the swamps. The lack of seedling establishment in the swamps may be due to the inability of seeds to find safe sites. At Myall Lakes, *B. aemula*, a dry heath species, failed to establish in nearby wet heath, even though experiments showed that seedlings were able to grow in this habitat. The lack of establishment in wet heath under natural conditions was attributed to insufficient soil disturbance, which reduced safe sites for seeds (Myerscough et al. 1996; Clarke et al. 1996). Little or no recruitment in the swamps would be expected if *B. spinulosa* seeds experience similar problems in finding safe sites.

If seeds of *B. spinulosa* germinated in the swamps, but seedlings died shortly afterwards, then they would not have been present when we surveyed the swamps 18 months after fire. Early mortality could have been mediated by abiotic conditions in the swamps. Compared with *B. marginata*, seedlings of *B. spinulosa* may lack the physiological capacity to cope with the poorly draining and often waterlogged swamp soils. Further, early seedling mortality could result from competitive exclusion. Seedlings of *B. spinulosa* grow more slowly than seedlings of *B. marginata* (Virgona 2004), and they may be unable to compete with the rapidly resprouting sedges in the swamps. Despite these potential obstacles, establishment of *B. spinulosa* in the swamps must occur occasionally as evidenced at SC by the presence of the small number of adult plants in this habitat. Given the ability of *B. spinulosa* plants to persist by resprouting, seedlings only need to be recruited rarely to maintain current plant densities.

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REFERENCES

Benson, D. and McDougall, L. (2000). Ecology of Sydney plant species 7b: Dicotyledon families Proteaceae to Rubiaceae. *Cunninghamia* 6, 1017-1198.

Benwell, A.S. (1998). Post-fire seedling recruitment in coastal heathland in relation to regeneration strategy and habitat. *Australian Journal of Botany* 46, 75-101.

Bowman, D.M.J.S., Maclean, A.R. and Crowden, R. K. (1986). Vegetation-soil relations in the lowlands of southwest Tasmania. *Australian Journal of Ecology* 11, 141-153.

Castro, J., Zamora, R., Hódar, J.A. and Gómez, J.M. (2004). Seedling establishment of a boreal tree species (*Pinus sylvestris*) at its southernmost distribution limit: consequences of being in a marginal Mediterranean habitat. *Journal of Ecology* 92, 266-277.

Clarke, P.J. (2002). Habitat insularity and fire response traits: evidence from a sclerophyll archipelago. *Oecologia* 132, 582-591.

Clarke, P.J., Myerscough, P.J. and Skelton, N.J. (1996). Plant coexistence in coastal heaths: Between- and within- habitat effects of competition, disturbance and predation in the post-fire environment. *Australian Journal of Ecology* 21, 55-63.

Enright, N.J., Lamont, B.B. and Marsula, R. (1996). Canopy seed bank dynamics and optimum fire regime for the highly serotinous shrub, *Banksia hookeriana*. *Journal of Ecology* 84, 9-17.

Grime, J.P. (1979). 'Plant strategies and vegetation processes'. (Wiley and Son: Chichester).

Groeneveld, J., Enright, N.J., Lamont, B.B. and Wissel, C. (2002). A spatial model of coexistence among three *Banksia* species along a topographic gradient in fire-prone shrublands. *Journal of Ecology* 90, 762-774.

Groom, P.K., Froend, R.H., Mattiske, E.M. and Gurner, R.P. (2001). Long-term changes in vigour and distribution of *Banksia* and *Melaleuca* overstorey species in the Swan Coastal Plain. *Journal of the Royal Society of Western Australia* 84, 63-69.

Grubb, P. (1977). The maintenance of species richness in plant communities: The importance of the regeneration niche. *Biological Review* 52, 107-145.

Hammill, K., Bradstock, R. and Allaway, W. (1998). Post-fire seed dispersal and species re-establishment in Proteaceous heath. *Australian Journal of Botany* 46, 407-419.

Harden, G.J. (2002). 'Flora of New South Wales'. Vol II.

(University of New South Wales Press, Sydney).

Harper, J.L. (1977). 'Population biology of plants'. (Academic Press: London).

Keith, D.A. and Myerscough, P.J. (1993). Floristics and soil relations of upland swamp vegetation near Sydney. *Australian Journal of Ecology* 18, 325-344.

Lamont, B.B., Enright, N.J. and Bergl, S.M. (1989). Coexistence and competitive exclusion of *Banksia hookeriana* in the presence of congeneric seedlings along a topographic gradient. *Oikos* 56, 39-42.

Lamont, B.B. and Groom, P.K. (1998). Seed and seedling biology of the woody-fruited Proteaceae. *Australian Journal of Botany* 46, 387-406.

Lamont, B.B. and Wiens, D. (2003). Are seed set and speciation rates always low among species that resprout after fire, and why? *Evolutionary Ecology* 17, 277-292.

Morrison, D.A., Cary, G.J., Pengelly, S.M., Ross, D.G., Mullins, B.J., Thomas, C.R. and Anderson, T.S. (1995). Effects of fire frequency on plant species composition of sandstone communities in the Sydney region: Inter-fire interval and time-since-fire. *Australian Journal of Ecology* 20, 239-247.

Mustart, P.J. and Cowling, R.M. (1993). The role of regeneration stages in the distribution of edaphically restricted Fynbos Proteaceae. *Ecology* 74, 1490-1499.

Myerscough, P.J., Clarke, P.J. and Skelton, N.J. (1995). Plant coexistence in coastal heaths: Floristic patterns and species attributes. *Australian Journal of Ecology* 20, 482-493.

Myerscough, P.J., Clarke, P.J. and Skelton, N.J. (1996). Plant coexistence in coastal heaths: Habitat segregation in the post-fire environment. *Australian Journal of Ecology* 21, 47-54.

Quinn, G.R. and Keough, M.J. (2002). 'Experimental design and data analysis for biologists'. (Cambridge University Press, Cambridge).

Schütz, W., Milberg, P. and Lamont, B.B. (2002). Germination requirements and seedling responses to water availability and soil type in four eucalypt species. *Acta Oecologica* 23, 23-30.

Sheringham, P. and Hunter, J.T. (2002). 'Vegetation and floristics of Gibraltar Range National Park'. (NSW National Parks and Wildlife Service, Glen Innes).

Siddiqi, M.Y., Carolin, R.C. and Anderson, D.J. (1972). Studies in the ecology of coastal heath in New South Wales. I. Vegetation structure. *Proceedings of the Linnean Society of New South Wales* 97, 211-224.

Sivertown, J. and Charlesworth, D. (2001). 'Introduction to plant population biology'. 4th edition, (Blackwell Science, Oxford).

Vaughton, G. and Carthew, S.M. (1993). Evidence for selective abortion in *Banksia spinulosa* (Proteaceae). *Biological Journal of the Linnean Society* 50, 35-46.

Vaughton, G. and Ramsey, M. (1998). Sources and consequences of seed mass variation in *Banksia marginata* (Proteaceae). *Journal of Ecology* 86, 563-573.

Vaughton, G. and Ramsey, M. (2001). Relationship between seed mass, seed nutrients, and seedling

growth in *Banksia cunninghamii* (Proteaceae). *International Journal of Plant Sciences* **162**, 599-606.

Vaughton, G. and Ramsey, M. (2006). Selfed seed set and inbreeding depression in obligate seeding populations of *Banksia marginata. Proceedings of the Linnean Society of New South Wales* **127**, 19-26.

Virgona, S.P. (2004). Habitat segregation of *Banksia marginata* and *B. spinulosa*. BSc Honours thesis, Botany, University of New England, Armidale.

Williams, P.R. and Clarke, P.J. (1997). Habitat segregation by serotinous shrubs in heaths: Post-fire emergence and seedling survival. *Australian Journal of Botany* **45**, 31-39.

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